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A review of the genus *Semele* (Ruscaceae) systematics in Madeira

MIGUEL ÂNGELO ALMEIDA PINHEIRO DE CARVALHO[1*], CHRISTOPHER CHARLES WILCOCK[2], TERESA MARIA MARQUES DOS SANTOS[1], IOLANDA CATARINA VALE LUCAS[1], JOSÉ FILIPE TEIXEIRA GANANÇA[1], EMANUEL FRANCO[1], DEVARAJAN THANGADURAI[1], DOULATHABAD MURALIDHARA RAO[3] and NÉLIA FREITAS SOUSA[1]

[1]*ISOPlexis Banco de Germoplasma, Centro de Estudos da Macaronésia, Universidade da Madeira, 9000–390 Funchal, Portugal*
[2]*Department of Plant and Soil Sciences, University of Aberdeen, Aberdeen AB24 3UU Scotland, UK*
[3]*Department of Biotechnology, Sri Krishnadevaraya University, Anantapur 515003, Andhra Pradesh, India*

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The present study attempts to review the systematics of *Semele* (Ruscaceae) in Madeira, based on phenotypic diversity. The variation in some vegetative (climbing shoot, second-order branches or 'phylloclades') and sexual (inflorescence and flowers) characters was analysed in 115 plant specimens from 30 field populations, herbaria of the Costa collection and Madeira Botanical Garden (MADJ) and certain gardens. Thirty-one quantitative and qualitative characters have been utilized in the analysis. Kaiser–Meyer–Olkin (KMO) analysis indicates adequate sampling. Principal component analysis (PCA) reveals that the spatial distribution of individuals has a discontinuous behaviour. Principal coordinate analysis (PCO) utilizing the Gower coefficient on standardized data revealed a significantly discontinuous distribution of individuals, such that two different clusters can be defined. The Student's *t*-test and Tukey test on separate characters, when individuals were classified according to the Costa classification, confirms the significant differences between grouping accessions. This leads to the recognition of two species within the genus in Madeira. Literature and herbarium studies show that these two taxa are conspecific with *Semele androgyna* (L.) Kunth *sensu stricto (s.s.)* and *Semele menezesi* Costa *sensu lato (s.l.)*. A separated statistical analysis of the *S. androgyna* cluster shows the possible existence of additional subgroups. Based on field population distribution, ecological behaviour and variation in features, we propose the recognition of two species, *S. androgyna* (L.) Kunth and *S. menezesi* (Costa) Pinheiro de Carvalho, and two subspecies *S. androgyna* (L.) Kunth *androgyna* Pinheiro de Carvalho and *S. androgyna* (L.) Kunth *pterygophora* Pinheiro de Carvalho.

ADDITIONAL KEYWORDS: morphological variation – *Semele androgyna* – *S. menezesi* – species differentiation.

INTRODUCTION

Semele (Kunth, 1842) is a palaeoendemic genus that occurs on the archipelagos of Madeira and the Canary Islands (Favarger & Contandriopoulos, 1961; Favarger, 1967; Kunkel, 1976). On the Canary Islands, *Semele* occurs throughout Gran Canaria, Tenerife, Gomera, Hierro and La Palma (Hansen & Sunding, 1993). On Madeira (Fig. 1), *Semele androgyna s.l.* occurs on Madeira (Hansen & Sunding, 1993), Deserta Grande (Costa Neves, Silva & Palmeira, 1992) and Porto Santo (Pickering, 1962; Roberto, Fontinha & Fernandes, 1998). However, the largest field distribution is in the Laurisilva and its transition zones of Madeira (Sjogren, 1972; Vieira, 1992; Vickery, 1994; Vale Lucas, Pinheiro de Carvalho & Paiva, 1998).

Semele is a rhizomatous, climbing genus of the Ruscaceae with an unusual morphology and particular terminology. The rhizome is sympodially branched with short internodes (sympodial units) and reduced

*Corresponding author. E-mail: quercus@uma.pt

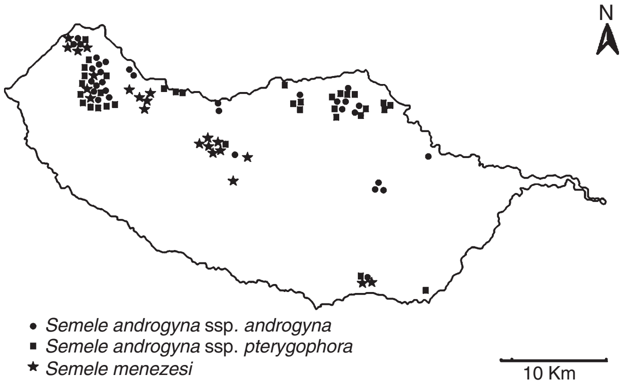

Figure 1. Map of Madeira, showing the principal island of the Archipelago of Madeira where the study was undertaken. The symbols represent the studied field populations of *Semele* and the distribution of the proposed taxa: *Semele androgyna* (L.) Kunth ssp. *androgyna* P. de Carvalho; *S. androgyna* (L.) Kunth ssp. *pterygophora* (Costa) P. de Carvalho and *S. menezesi* (Costa) P. de Carvalho.

scale leaves (= bracts). Sympodial units develop aerial shoots. The main aerial shoot (= *sarmento*) has second-order branches (= *sarmenticulo*), bearing phylloclades (= *cladodes*) and inflorescences (= *glomerules*). Phylloclades of fertile or infertile types represent dorsiventrally flattened perennial, coriaceous stems (Cooney-Sovetts & Sattler, 1986; Vale Lucas *et al.*, 1998). Inflorescences are normally displayed on the margins of phylloclades, although an abaxial disposition can also be detected. Monoecious flowers are usually produced, with reduced male or female functions. A detailed plant description can be found in several works (Kunth, 1850; Costa, 1927, 1949, 1950; Cooney-Sovetts & Sattler, 1986; Vale Lucas, Pinheiro de Carvalho & Paiva, 1994, 1998; Vickery, 1994).

The plant was first described by Linnaeus (Linnaeus, 1753; Medicus, 1787; Link, 1829). Kunth (1842) described the genus and later a species (1850) common to both Madeira and the Canary Islands, *Semele androgyna* (L.) Kunth [= *Ruscus androgynus* L.]. Later a new taxon, *Semele gayae* (Webb) Svent et Kunk. [= *Danae gayae* Webb; = *S. androgyna* (L.) Kunth var. *gayae* (Webb) Burch.], was recognized from Gran Canaria (Webb, 1847; Ciferri, 1962; Kunkel & Sventenius, 1972; Kunkel, 1976; Hansen & Sunding, 1993). However, the systematics of *Semele* in Madeira is less well known.

Morphological variability has been analysed several times (Menezes, 1922; Costa, 1927, 1949, 1950; Vale Lucas *et al.*, 1994, 1998; Vickery, 1994; Pinheiro de Carvalho *et al.*, 2001). Costa (1927, 1949, 1950) examined the genus in Madeira and proposed several new specific (four species) and subspecific (one subspecies and 11 varieties) taxa. However, later botanists have not recognized these taxa (Hansen & Sunding, 1993; Vickery, 1994), and they are considered to be based on slightly abnormal individuals. Vickery (1994) recognized only one species within the genus, *Semele androgyna* (L.) Kunth. Several other arguments have been presented against Costa's taxonomy, such as the variability of plants growing in different environmental conditions and the lack of constancy of the utilized characters (Vickery, 1994). Thus despite these early studies in Madeira, the morphological variability of *Semele* needs to be reassessed and its taxonomic significance reanalysed (Vale Lucas *et al.*, 1998).

Recently various aspects of the *Semele* biology have been reanalysed (Cooney-Sovetts & Sattler, 1986; Sattler, 1988; Vale Lucas *et al.*, 1998; Rudall & Campbell, 1999). Cooney-Sovetts & Sattler (1986) on studying *Semele* ontogeny showed that the plant has a very constant development. They showed that developmental abnormalities are confined to the abnormal disposition of branches and phylloclades, the bearing of secondary phylloclades on the main ones or the formation of separate terminal stalks with inflorescences. These data agree with our observations on the plant's biological cycle and development (Vale Lucas *et al.*, 1998). During the initial phase of development, the aerial part is composed of several leaf-like primary phylloclades. The first main aerial shoot appears after four or five years of vegetative development. Shoots have an annual extensive growing cycle, during which they present pre-established developmental features, with a determined number of second-order branches, non-fertile or fertile phylloclades. Two different growing behaviours of main shoots can be detected among *Semele* plants. Fertile phylloclades are developed on the second-order branches or in some cases in the apical areas of the main shoot and higher second-order branches. Apices of inflorescences in fertile phylloclades are initially present, but their development starts only during the second or third year of the main shoot vegetative cycle. The number of inflorescences is pre-established and each is composed of a group of buds of different size, number of flowers and flowering features. Two different flowering behaviours are also detected among *Semele* plants (Vale Lucas *et al.*, 1998).

However, some of this recent work must be questioned because of the lack of understanding of the morphological variability of this genus. For example, Rudall & Campbell (1999) report that *Semele* pollen is inaperturate, but this is inconsistent with most monocotyledons, which are monosulcate. We have shown that *Semele* pollen is monosulcate (Vale Lucas *et al.*, 1998) and that the error arose because Rudall & Campbell studied inviable pollen from functionless anthers in female flowers of *Semele androgyna.*

According to Cooney-Sovetts & Sattler's (1986) data, Costa (1950), in his *Semele* classification, only partially utilized some plant developmental abnormalities. Later work based on morphological and newly examined anatomical characters has suggested that the genus in Madeira needs to be re-examined taxonomically (Cooney-Sovetts & Sattler, 1986; Sattler, 1988; Vale Lucas *et al.*, 1994, 1998). Re-examination of the same morphological characters used by Costa (1949, 1950) confirms that some are highly variable, and their taxonomic importance over-emphasized. Despite this, it has been observed that several features, in particular inflorescence structure and fertile phylloclades dispositions, seem to suggest the existence of distinct morphological types within the genus (Vale Lucas *et al.*, 1998). The difficulties in delimiting taxa within *Semele* led us to apply statistical tools to evaluate its morphological variability. The present study aims to compare phenotypic variability, based on field samples, using statistical analysis of morphological and reproductive characters, to look for clear discontinuities in the variation and to compare the results with the available vouchers of Costa and MADJ herbarium collections. The characters utilized in this study have been fully discussed by Vale Lucas *et al.* (1998).

MATERIAL AND METHODS

One hundred and fifteen plant specimens, among them 89 field plants, 11 voucher specimens from Costa and 15 from MADJ herbarium collections, were studied. A small-scale population study approach was used, in which plants from field populations and herbarium collections were biometrically compared. In total 30 field populations from Madeira and 26 voucher specimens from Madeira were used for this study. Plant specimens were selected with the aim of including the greatest range of observable diversity in the field. Only adult and flowering plants have been included in the present study. Distribution and ecology of studied specimens was also established. Apart from the Costa reference specimens, only herbarium material in good condition, flowering, and with well-defined locality data, which allowed a full biometrical analysis, were selected. Following these criteria, *Semele pterygophora* Costa reference specimens were excluded, because they were sterile or in bad condition. A voucher specimen from MADJ collection classified, as *S. pterygophora* Costa by the Madeiran botanist Nóbegra, MADJ number 07826, was included as an alternative. Voucher specimens of the field plants were deposited in the UMAD herbarium collection. An attempt to classify *Semele* accessions using some of the major Costa's characters was made, with the aim of testing Costa's taxonomy (Costa, 1927, 1949, 1950).

Morphological measurements were performed following Vale Lucas *et al.* (1998). However flower biometry, due to practical difficulties, was not included. Plants were analysed using 31 morphological and reproductive characters, 18 quantitative and 13 qualitative (Table 1; Fig. 2). Each measurement was made at least 15 times using an electronic ruler and the respective mean (M) and standard deviation (SD) was calculated.

Multivariate methods were used to summarize variation patterns produced by all characters or subsets of characters. The Kaiser–Meyer–Olkin (KMO) analysis was performed to determine the adequacy of *Semele* sampling. Principal components analysis (PCA) was used as an objective method to summarize variation, when prior knowledge of a population or taxonomic group to which individuals belonged is disregarded. Factor analysis of mean values, based on Eigen values was performed, using SPSS for Windows v. 10.0, following Kinnear & Gary (1999). Principal coordinates analysis (PCO), using Gower general similarity coefficients, was performed to summarize variation and discriminate the weight of qualitative characters, using MVSP for Windows v. 3.13d, following Kovach (1999). A canonical analysis of discriminance was employed to ordinate population means, considering variance and covariance among characters within and among plant groups. Student's *t*-tests were performed to evaluate the differences in values for single characters between the possible taxa. The *t*-tests, the calculations of mean values and standard deviations and discriminant analyses were performed using SPSS 10.0 for Windows (Kinnear & Gary, 1999; SPSS Inc., 1999). To perform multiple comparisons among pairs of means for all possible *Semele* groups, a Tukey test was performed using SPSS 10.0 for Windows (SPSS Inc. (1999). In this test, the significance level was $P < 0.05$. All character values were standardized and log-transformed prior to use in the multivariate analysis, as well as in the *t*-tests and the Tukey test.

RESULTS

Morphological analyses

The present study is based on fieldwork developed between 1994 and 2001. This period of time was necessary to detect some rare plant populations, which were classified as *S. menezesi* or *S. maderensis sensu* Costa, as well as to identify adult and flowering specimens in studied *Semele* populations. The long biological cycle of *Semele* plants was a limiting factor in this study. Table 1 and Figure 2 show the morphological characters analysed and their character states. Several characters utilized by Costa (1950)

Table 1. Morphological and reproductive characters analysed in all *Semele* accessions included in the present study. Characters were selected based on the analysis of Costa classification and our fieldwork observations

Parameter	Description	Type
MLS	Second-branch width (measured between the apical terminations of opposite phylloclades)	Quantitative
MCS	Second-branch length (measured between the apical termination and branch insertion in the main shoot)	Quantitative
CRSR	Second-branch width/length ratio	Quantitative
NCS	Number of phylloclades per second-order branch	Quantitative
MLCI	Lower phylloclades width (determined in the phylloclades near to the branch insertion in the main shoot)	Quantitative
MCCI	Lower phylloclades length (determined in the phylloclades near to the branch insertion in the main shoot)	Quantitative
CRCI	Lower phylloclades width/length ratio	Quantitative
MLCS	Upper phylloclades width (determined in the phylloclades near to the second-branch termination)	Quantitative
MCCS	Upper phylloclades length (determined in the phylloclades near to the second-branch termination)	Quantitative
CRCS	Upper phylloclades width/length ratio	Quantitative
NCF	Number of fertile phylloclades per second-order branch	Quantitative
RCR	Fertile phylloclades/total number of phylloclades ratio	Quantitative
NG	Number of inflorescence per fertile phylloclades	Quantitative
RCRG	Inflorescences/fertile phylloclades ratio	Quantitative
NF	Number of flowers per inflorescence	Quantitative
RCRFC	Flowers/fertile phylloclades ratio	Quantitative
RCRFI	Flowers/inflorescence ratio	Quantitative
CPE	Pedicel length	Quantitative
ECO	Ecological behaviour (1 – ubiquitous, 2 – moist, shady habitats)	Qualitative
CS	Main aerial shoot length (1 – lower 3 m, 2 – upper to 15 m)	Qualitative
VS	Behaviour of aerial shoot (1 – flattened, 2 – climbing and voluble)	Qualitative
TS	Main aerial shoot termination (1 – pair apical phylloclades (= bipinnate), 2 – one apical phylloclades (= monopinnate), 3 –flattened apex termination (= falsiform)	Qualitative
TTS	Second-order branch termination (1 – pair apical phylloclades (= bipinnate), 2 – one apical phylloclades (= monopinnate), 3 –flattened apex termination (= falsiform)	Qualitative
TCI	Shape of lower second branch phylloclades (determined by dropping the length by width: 1 – ovate-falsiform (variation 0–3); 2 – oblong-lanceolate (3–5); 3 – lanceolate (upper 5) shapes)	Qualitative
TCS	Shape of upper second branch phylloclades (similar to TCI classification)	Qualitative
PCL	Presence (1) or absence (2) secondary phylloclades	Qualitative
TIN	Inflorescence type (1 – small buds with up to 7 flowers, 2 – median buds with between 8 and 19 flowers, 3 – big buds with more than 20 flowers)	Qualitative
FCS	Fertile phylloclades disposition in the second-branch (1 –fertile phylloclades in lower part of second-branch, 2 – all or 2/3 phylloclades are fertile in the second branch, 3 – only apical phylloclades in second-branch and main shoot are fertile, 4 – apical and several (2–10) lower phylloclades in second-branch and main shoot are fertile)	Qualitative
DGC	Floral disposition in the fertile phylloclades (1 – marginal flowering, 2 – abaxial flowering present (nondominate), 3 –abaxial flowering)	Qualitative
NNG	Type of fertile phylloclades nervation (1 – absence of distinguish inflorescence nerve, 2 – one marginal inflorescence nerve, 3 – one central nerve with a terminal inflorescence, 4 – two marginal inflorescence nerves, 5 – two marginal and one central inflorescence nerves)	Qualitative
SF	Flower sex (1 – male flowers, 2 – female flowers, 3 – hermaphrodite flowers)	Qualitative

distinguish four *Semele* species, such as main shoot length (CS) and behaviour (VS), second-order branch termination (TTS), the presence or absence of secondary phylloclades (PCL), shape (TC) and number of phylloclades (NCS), as well as fertile phylloclades disposition (FCS) have been analysed in this study. All characters have been determined and measured in 115 *Semele* accessions. *Semele* accessions and their provenance are presented at the end of this work.

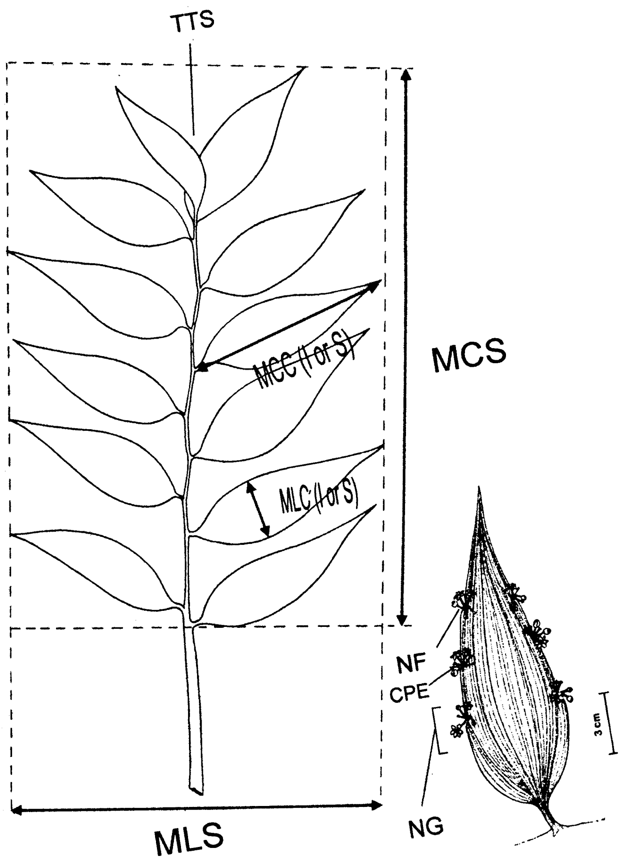

Figure 2. Picture of *Semele* second-order branch and phylloclades. The scheme represents some of the major morphological characters analysed during the present study. The abbreviations are presented according to Table 1.

Multivariate analyses

The KMO analysis performed for the variation of *Semele* accessions gives a value of 0.82, which indicates adequate plant sampling and allowed us to perform PCA analysis. In the PCA analysis, the *Semele* accessions were clustered into two main groups with discontinuity (Fig. 3A). In these analyses characters without variance have not been utilized. The separation along both PCA axes explains 55.8% of variation. The sum of Eigen values for axes 1 and 2 is 17.3 from a total of 24.7. Only the accession numbers, 79, 71 and 72, all voucher specimens of Costa's collection do not group into these clusters. In Figure 3B is shown the contribution of different variables to the *Semele* accessions separation. The reproductive characters such as NG, NCF, NCS and the vegetative VS and CS contribute most to the separation of accessions along PCA axis 1, while the vegetative characters, such as MLCS, MCCS, MCCI, MLS and MLCI contribute most to the separation along axis 2. PCO analyses using the Gower general similarity coefficient to discriminate qualitative characters also show the discontinuity of variation observed in *Semele* accessions, which cluster in to two groups (Fig. 3C). The sum of Eigen values for axes 1 and 2 is 18.1 from a total of 23.5. The third axis has been omitted due to an insignificant proportion of the total variation. The separation along both PCA and PCO axes explains 83.9 and 44.7%, respectively, of the variation. The discontinuity between both clusters in PCA plots is less clear than in the PCO analysis, but the studied *Semele* accessions clearly have a discontinuous variation of the studied characters. As result of PCO analysis only the accession number 79 remains placed between the main *Semele* groups. To evaluate the significance of this discontinuity, an analysis of Costa's (1950) systematic recommendations was performed. Six characters used by Costa (1949, 1950) – CS, VS, TTS, NCS, NG (number of inflorescences), and NF (number of flowers) – were utilized to classify *Semele* accessions into four major groups, which are *S. androgyna*, *S. pterygophora*, *S. maderensis*, *S. menezesi sensu* Costa (1949, 1950) and a multivariate analysis was performed. The results of these analyses are shown in Figure 4A, B where accessions recognized as *S. androgyna* and *S. pterygophora* all form one major cluster, while the remaining accessions classified as *S. maderensis* and *S. menezesi* are grouped in the other cluster. The single accession classified as *S. tristonis* is a voucher specimen from the Costa collection. No population or specimen with the same morphological features described for *S. tristonis* was observed in nature during the present study. Based on this distribution, a re-evaluation of *Semele* published and unpublished nomenclature is proposed.

Fieldwork observations revealed that eight plant reproductive characters, as well as the number of phylloclades per second-order branch seem to be determining accessions and *Semele* phenotypic variability. These characters were evaluated by performing PCA and PCO analyses of *Semele* accessions (Fig. 5A–C), which also gives a clustering of *Semele* accessions in two major groups. The PCA separation along the axes explains 84.0% of variation and has Eigen values of 7.6. The PCO separation along the axes explains 44.7% of variation and has Eigen values of 18.1 on a total of 23.5. From this analysis it is evident that reproductive characters are very effective in distinguishing *Semele* taxa.

The multivariate PCA and PCO analyses of separated *Semele* subsets were performed using all variables, as well as major reproductive characters, to determine the existence of different *Semele* subgroups and to evaluate Costa's taxa. The results show that the *S. androgyna*, but not the *S. menezesi* cluster, can be differentiated into two smaller clusters. However, an overlap of different accessions exists between these groups (Fig. 4A, B).

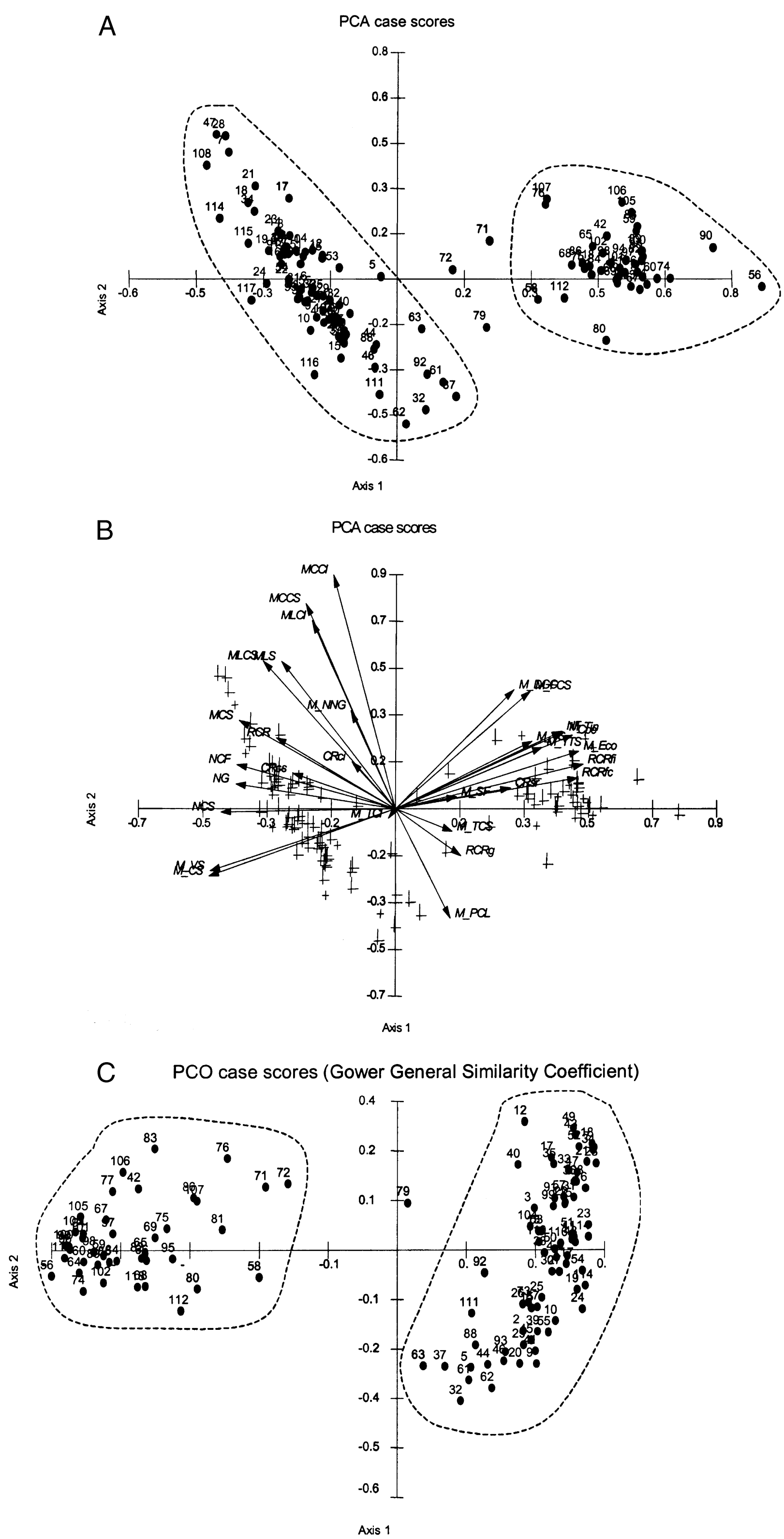

Figure 3. A, B, principal component analysis (PCA) on the 115 *Semele* accessions based on all characters. PCA variation explained along the first axis is 44.2% and 11.6% along the second axis. The contributions of single characters are shown in the PCA biplot graph. C, principal coordinates analysis (PCO) on the 115 *Semele* accessions based on all characters. PCO variation explained along the first axis is 37.1% and along the second axis is 7.6%.

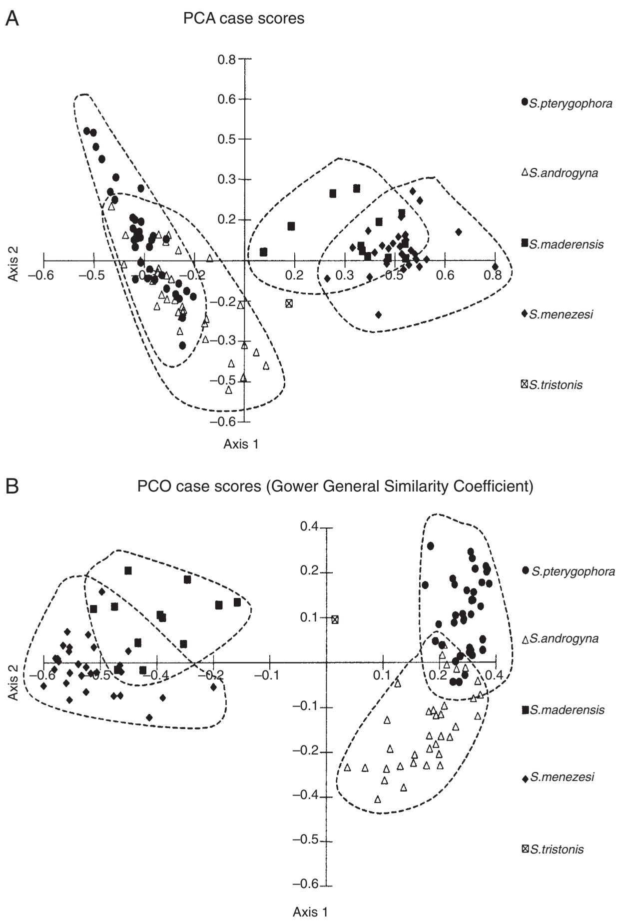

Figure 4. A, principal component analysis and B, principal coordinate analysis of 115 *Semele* accessions based on all variables. Variation explained by the axis of both plots is the same as in Fig. 3. The *Semele* accessions are classified according to the Costa nomenclature based on six major Costa characters (Costa, 1949, 1950).

Comparisons of means in single characters

In the *t*-test performed on all studied accessions (Table 2), all quantitative characters except lower phylloclades ratio (CRCI) showed a significant difference between *S. androgyna* and *S. menezesi*. In the *t*-test for *S. androgyna* cluster accessions only (Table 3), the characters CRCI and upper phylloclades ratio (CRCS) did not show a significant difference between *S. androgyna* and *S. pterygophora*. The *t*-test for *S. menezesi* cluster accessions showed no significant differences between *S. menezesi* and *S. maderensis* (Table 4). Overall, these results confirm the detachedness of both *S. androgyna* and *S. menezesi*. In Table 5 are summarized the results of a Tukey test that show the differences between all possible taxa. These differences in morphological characters, as well as ecological distribution of accessions allow us to propose the separation of *S. androgyna* (L.) Kunth into *S. androgyna* (L.) Kunth *s.s. and S. menezesi s.l.* (Costa) Pinheiro de Carvalho, and the subdivision of *S. androgyna* into *S. androgyna* (L.) Kunth subsp *androgyna* and *S. androgyna* (L.) Kunth subsp. *pterygophora* Pinheiro de Carvalho.

Systematic considerations of *Semele*

Semele androgyna (L.) Kunth ssp. *androgyna* Pinheiro de Carvalho in *Proc. Island Ecosys. Con. Mol. Appr.* 1: 218 (2001)

Ruscus androgynus L.; *S. androgyna* (L.) Kunth; *S. tristonis* J.G. Costa; *S. androgyna* (L.) Kunth var. *macrophyla* Menezes; *S. androgyna* (L.) Kunth var. *laxa* J.G. Costa; *S. androgyna* (L.) Kunth var. *conferta* J.G. Costa.

Rhizomatous climbers, up to 12 m, composed by variable number of second-order branches and a pair of reduced phylloclades in the termination, phylloclades 18 (11–30) per secondary branch, phylloclades vegetative or fertile, 8 (1.5–14.5) fertile phylloclades, rare apical ones, lower phylloclades 1.2–5.4 × 5.5–13.6 cm, distal phylloclades, 2.0–7.7 × 7.5–17.6 cm, green slightly coriaceous, parallel nerves, with perpendicular veins. Leaves 3.0–4.0 × 1.1–1.6 cm, cuneiform, green with violet pigmentation. Inflorescences usually 3 (1.2–9.6) per phylloclades, non-globular, marginal. Flowers usually 4 (2.0–6.3), unisexual or hermaphrodite, pedicel, 0.4 (0.3–0.5) mm, flower sizes 9–12 mm diameter. Fruit an orange red berry. Seeds have spherical shape and hard not farinaceous endosperm. Testa without phytomelan and pale.

Semele androgyna (L.) Kunth ssp. *pterygophora* (J.G. Costa) Pinheiro de Carvalho in *Proc. Island Ecosys. Con. Mol. Appr.* 1: 218 (2001)

S. pterygophora J.G. Costa; *S. pterygophora* var. *dolichoclados* J.G. Costa; *S. pterygophora* var. *congeminata* J.G. Costa; *S. pterygophora* var. *elegantissima* J.G. Costa; *S. pterygophora* var. *barretiana* J.G. Costa.

Key to studied taxa of *Semele*

1. Aerial erect shoots, inflorescence globular, number of flowers 20 or more .... *S. menezesi*
1. Aerial climbing shoots, inflorescence nonglobular, number of flowers less than 20
   2. Slightly coriaceous phylloclades, flowers 4 .... *S. androgyna* ssp. *androgyna*
   2. Very coriaceous phylloclades, flowers 6 .... *S. androgyna* ssp. *pterygophora*

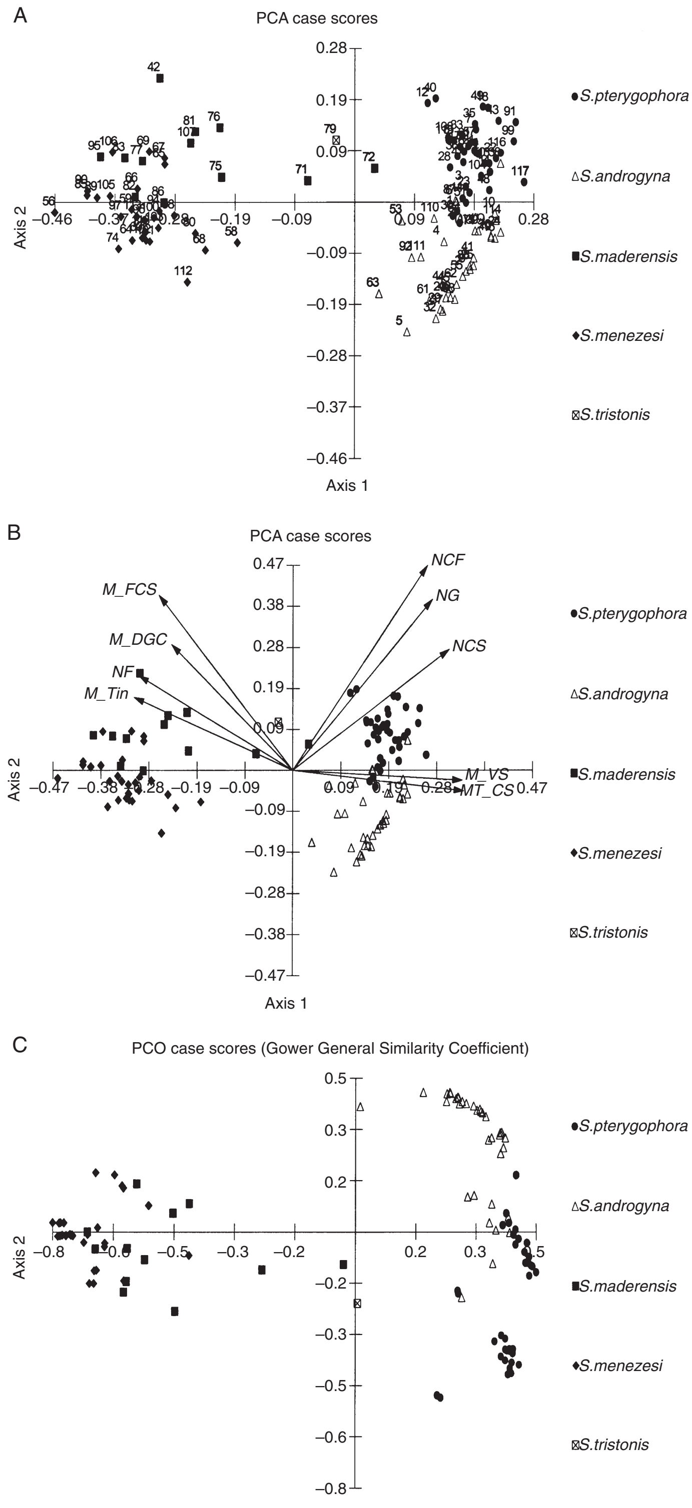

Figure 5. A, B, principal component analysis (PCA) on the 115 *Semele* accessions based only on reproductive characters. PCA variation explained along the first axis is 71.0% and along the second axis is 13.0%. The contributions of single characters are shown in the PCA biplot graph. C, principal coordinates analysis on the 115 *Semele* accessions based only on reproductive characters. PCO variation explained along the first axis is 37.1% and along the second axis is 7.6%. The *Semele* accessions are classified according to the Costa nomenclature based on six major Costa characters (Costa, 1949, 1950).

Table 2. Range of variation in the quantitative characters of *Semele* accessions. The mean ± SD for each character and mean values were tested with a Student's *t*-test. Characters 2, 3, 6, 7, 9 and 10 are given in centimetres, and character 13 in millimetres

	S. androgyna		*S. menezesi*		
Character	*N*	Mean ± SD	*N*	Mean ± SD	Significance
1 CRSR	74	0.5 ± 0.14	41	0.8 ± 0.05	***
2 MLS	74	25.0 ± 6.70	41	19.0 ± 0.85	***
3 MCS	74	56.8 ± 21.90	41	28.1 ± 1.54	***
4 NCS	74	21.1 ± 4.56	41	10.1 ± 0.71	***
5 CRCI	74	0.3 ± 0.01	41	0.3 ± 0.01	NS
6 MLCI	74	3.3 ± 1.13	41	2.7 ± 0.08	**
7 MCCI	74	10.7 ± 2.81	41	9.9 ± 0.22	*
8 CRCS	74	0.4 ± 0.08	41	0.3 ± 0.01	***
9 MLCS	74	4.5 ± 1.58	41	3.0 ± 0.01	***
10 MCCS	74	12.4 ± 3.00	41	10.8 ± 0.25	***
11 NG	74	4.8 ± 2.77	41	1.2 ± 0.07	***
12 NF	74	4.3 ± 1.49	41	20.0 ± 1.99	***
13 CPE	74	0.4 ± 0.10	41	1.0 ± 0.02	***
14 NCF	74	13.1 ± 6.49	41	4.0 ± 0.69	***
15 RCR	74	0.6 ± 0.22	41	0.4 ± 0.04	***
16 RCRFC	74	0.5 ± 0.05	41	10.0 ± 1.59	***
17 RCRG	74	0.4 ± 0.03	41	0.6 ± 0.05	***
18 RCRFI	74	1.2 ± 0.10	41	18.1 ± 1.93	***

Significance levels: NS, $P \geq 0.05$; *$P < 0.05$; **$P < 0.01$; ***$P \leq 0.001$

Table 3. Range of variation in the quantitative characters of *Semele androgyna* and *S. pterygophora* accessions. The mean ± SD for each character and mean values were tested with a Student's *t*-test. Characters 2, 3, 6, 7, 9 and 10 are given in centimetres, and character 13 in millimetres

	S. androgyna		*S. pterygophora*		
Character	*N*	Mean ± SD	*N*	Mean ± SD	Significance
1 CRSR	35	0.5 ± 0.16	38	0.4 ± 0.09	*
2 MLS	35	22.8 ± 5.68	38	27.5 ± 6.56	**
3 MCS	35	45.4 ± 16.17	38	67.6 ± 21.41	***
4 NCS	35	18.2 ± 3.79	38	23.7 ± 3.57	***
5 CRCI	35	0.3 ± 0.07	38	0.3 ± 0.07	NS
6 MLCI	35	3.1 ± 1.13	38	3.5 ± 1.22	*
7 MCCI	35	9.6 ± 2.02	38	11.8 ± 3.05	***
8 CRCS	35	0.4 ± 0.07	38	0.4 ± 0.08	NS
9 MLCS	35	4.2 ± 1.29	38	4.9 ± 1.73	*
10 MCCS	35	11.5 ± 2.51	38	13.4 ± 3.14	***
11 NG	35	3.0 ± 1.85	38	6.4 ± 2.46	***
12 NF	35	3.8 ± 1.20	38	4.7 ± 1.53	*
13 CPE	35	0.4 ± 0.06	38	0.4 ± 0.11	**
14 NCF	35	7.7 ± 3.62	38	18.7 ± 4.17	***
15 RCR	35	0.4 ± 0.16	38	0.8 ± 0.11	***
16 RCRFC	35	0.7 ± 0.56	38	0.3 ± 0.07	***
17 RCRG	35	0.5 ± 0.35	38	0.4 ± 0.12	***
18 RCRFI	35	1.5 ± 0.75	38	0.8 ± 0.38	***

Significance levels: NS, $P \geq 0.05$; *$P < 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$

Table 4. Range of variation in the quantitative characters of *Semele menezesi* and *S. maderensis* accessions. The mean ± SD for each character and mean values were tested with a Student's *t*-test. Characters 2, 3, 6, 7, 9 and 10 are given in centimetres and character 13 in millimetres

	S. maderensis		S. menesezi		
Character	*N*	Mean ± SD	*N*	Mean ± SD	Significance
1 CRSR	12	0.6 ± 0.25	29	0.9 ± 0.33	NS
2 MLS	12	19.2 ± 6.11	29	18.9 ± 5.26	NS
3 MCS	12	37.2 ± 10.11	29	24.4 ± 7.04	**
4 NCS	12	13.6 ± 6.39	29	8.7 ± 2.52	NS
5 CRCI	12	0.3 ± 0.05	29	0.3 ± 0.62	NS
6 MLCI	12	2.7 ± 0.45	29	2.8 ± 0.50	NS
7 MCCI	12	10.1 ± 1.39	29	9.8 ± 1.46	*
8 CRCS	12	0.3 ± 0.05	29	0.3 ± 0.07	**
9 MLCS	12	2.7 ± 0.44	29	3.1 ± 0.67	NS
10 MCCS	12	11.0 ± 1.84	29	10.7 ± 1.53	NS
11 NG	12	1.5 ± 0.67	29	1.1 ± 0.21	NS
12 NF	12	20.2 ± 11.36	29	19.9 ± 13.44	NS
13 CPE	12	1.0 ± 0.19	29	1.1 ± 0.12	NS
14 NCF	12	9.2 ± 5.26	29	1.9 ± 1.10	**
15 RCR	12	0.7 ± 0.18	29	0.2 ± 0.11	NS
16 RCRFC	12	3.2 ± 2.52	29	12.9 ± 10.82	*
17 RCRG	12	1.9 ± 0.07	29	0.7 ± 0.28	NS
18 RCRFI	12	16.5 ± 11.33	29	18.8 ± 12.91	**

Significance levels: NS, $P \geq 0.05$; *$P < 0.05$; **$P \leq 0.01$.

Table 5. Mutiple comparisons among pairs of means between all pair of *Semele* taxa according to Costa classification (1950), using the Tukey test. Abbreviations: 1, *S. androgyna s.s.*; 2, *S. pterygophora*; 3, *S. menezesi*; 4, *S. maderensis*. Characters are abbreviated according to Table 1

Semele taxa	Significant characters[1]	Non-significant characters
1 and 2	MLS, MCS, NCS, MCCI, MCCS, NG, NCF, RCR	RCRFC, RCRFI, MLCI, RCRG, CPE, NF, MLCS, CRCS, CRSR
1 and 3	MCS, NCS, CRCS, MLCS, NF, CPE, RCR, RCRG, RCRFI	RCRFC, NCF, NG, MLS, MLCI, MCCS, MCCI, CRSR
1 and 4	CRSR, MLS, MCS, NCS, CRCS, MLCS, NG, NF, CPE, NCF, RCR, RCRFC, RCRG, RCRFI	MLCI, MCCS, MCCI
2 and 3	MLS, MCS, NCS, MLCI, MCCI, CRCS, MLCS, MCCS, NG, NF, CPE, NCF, RCRFI	RCRFC, RCR, RCRG,CRSR
2 and 4	CRSR, MLS, MCS, NCS; MLCI, CRCS, MLCS, MCCS, NG, NF, CPE, NCF, RCR, RCRFC, RCRG,RCRFI	MCCI
3 and 4	CRSR, NCS, NCF, RCR, RCRFC, RCRG	MCS, NG, MLS, RCRFI, MLCI, CPE, NF, MCCS, MLCS, CRCS, MCCI

[1]Significance level $P < 0.05$.

Rhizomatous climbers, up to 18 m, compose by variable number of second-order branches and a pair of reduced phylloclades in the termination, phylloclades 24 (17–30) per secondary branch, phylloclades vegetative or fertile, 18 (10.3–25.3) fertile phylloclades, frequently all fertile, lower phylloclades 2.0–6.5 × 6.7–18.3 cm, distal phylloclades 2.7–9.9 × 7.4–22.8 cm, ovate-lanceolate, frequently bifurcated, very coriaceous, velvety parallel nerves, with prominent 2 marginal floral nerves. LEAVES 2.8–3.5 × 1.1–1.5 cm, cuneiform, green with violet pigmentation. INFLORESCENCES usually 7 (3.9–14.5) per phylloclade, nonglobular, marginal, very rare abaxial. FLOWERS usually 6 (3.4–8.9), unisexual or rare hermaphrodites, pedicel, 0.4 (0.2–0.7) mm, flower sizes 9–13 mm diameter. FRUIT red berry. SEEDS have spherical shape and hard not farinaceous endosperm. TESTA without phytomelan and pale.

Semele menezesi (J.G. Costa) Pinheiro de Carvalho

S. menezesi J.G. Costa; *S. menezesi* var. *carinata* J.G. Costa; *S. menezesi* var. *grabhamii* J.G. Costa; *S. menezesi* subvar. *prolixa* J.G. Costa; *S. maderensis* J.G. Costa; *S. maderensis* subvar. *presbytera* J.G. Costa; *S. maderensis* ssp. *portumonizensis* J.G. Costa

Rhizomatous, erect aerial shoots, up to 3 m, composed by variable number of small second-order branches and upper part with simple well formed phylloclades and monophylloclade or flattened axes in the termination, rarely a pair of phylloclades, phylloclades usually 10 (4.5–28.0), per secondary branch, phylloclades vegetative or fertile, usually 1–4 fertile, frequently the apical in the second-order branches and aerial shoots, rare in other lower phylloclades, lower phylloclades 1.0–3.8 × 7.4–14.2 cm, distal phylloclades, 1.7–4.3 × 8.0–14.8 cm, ovate-lanceolate, frequently bifurcated, very coriaceous, velvety, parallel nerves, with 1 or 2 prominent floral nerves. LEAVES 1.0–2.3 × 0.8–1.3 cm, cuneiform, green with violet pigmentation. Inflorescences usually 1–3 per phylloclade, globular, abaxial or marginal. FLOWERS usually 20 (5–49), unisexual, pedicel, 1.0 (0.7–1.4) mm, flower 11–18 mm diameter. SEEDS have spherical shape and hard not farinaceous endosperm. TESTA without phytomelan and pale.

DISCUSSION

The statistical analysis of morphological data of 115 *Semele* accessions supports the existence of multiple taxonomic units in Madeira. These results support the view of earlier authors (e.g. Menezes, 1922; Costa, 1927, 1949, 1950). At the same time, these results are contrary to the recognition of a single species inside the genus (Hansen & Sunding, 1993; Vickery, 1994). Previously, we have pointed out the existence of two *Semele* morphological types based on the analysis of morphological variation, reproductive features and different ecology of field diversity (Vale Lucas *et al.*, 1998; Pinheiro de Carvalho *et al.*, 2001). The present work further supports this hypothesis and the presence of two major clusters inside the genus (Fig. 3). From this we conclude that these morphological types deserve recognition at the species level. Proposed *Semele* species on the Madeira are *S. androgyna s.s.* Kunth (1850) and *S. menezesi* Costa (1927). This last species corresponds to a description of *S. menezesi s.l.*, when compared with Costa's systematics (Costa, 1927, 1949, 1950) and the species type specimens are deposited in the Herbarium of the Municipal Museum of Funchal. The taxa are separated on morphological features (Costa, 1927, 1949, 1950; Vale Lucas *et al.*, 1998; Pinheiro de Carvalho *et al.*, 2001). The phylloclade and its morphological features (form, number, shape) were commonly used in *Semele* taxonomy by Costa (1927, 1949, 1950), but were reviewed by Vickery (1994). This work shows that the principal aerial shoots and second-order branch sizes and termination, shape, number and insertion of inflorescence, and flower number and flowering behaviour can be used to discriminate different taxa. These characters allow us to clearly distinguish *S. androgyna* and *S. menezesi*. Additionally, both taxa differ in their distribution and ecology (Pinheiro de Carvalho *et al.*, 2001).

The *S. androgyna* cluster has been shown to be composed of two groups, which tend to be separated on the basis of their vegetative features viz. secondary stems or phylloclade sizes and shapes, or reproductive features, viz. inflorescence and flower numbers. One of these groups corresponds to *S. pterygophora* recognized as a species by Costa (1950). The significant differences in the plant characters detected by the *t*-test allow us to propose the differentiation of two subspecies. Although these subspecies have similar ecological and geographical distributions, preliminary data point to significant biochemical differences in *S. androgyna* (L.) Kunth *s.s*. The subspecies type specimens are included in the collection of Herbarium of the Municipal Museum of Funchal. Within the *S. menesezi* cluster, our data do not support the separation of different species following Costa (1927, 1950).

CONCLUSIONS

Our results allow us to conclude that the genus in Madeira is not monospecific, instead we recognize two species, *S. androgyna* (L.) Kunth *s.s.* and *S. menezesi* (Costa) Pinheiro de Carvalho *s.l.* We propose two subspecies inside *S. androgyna* (L.) Kunth ssp. *androgyna* Pinheiro de Carvalho and ssp. *pterygophora* (Costa) Pinheiro de Carvalho. Our analyses of *S. menezesi* showed that the observed variability was not enough to differentiate other taxa. Reference voucher specimens of proposed species and subspecies are included in Costa's and Madeira University herbarium collections. Further molecular studies will be undertaken to compare with the morphological variation to assess relationships between the Madeiran and Canary Island taxa.

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APPENDIX

Systematics of the genus *Semele* (Ruscaceae) in Madeira. The table shows the accessions studied in the present work, their numbers, field localization, herbarium localizations, and voucher specimen numbers, collector names, date of collection and accepted names. UMAD, Madeira University Herbarium; MADM, Municipal Museum of Funchal Herbarium; MADJ, Botanical Garden Herbarium.

No.	Locality	Voucher number	Collector	Date of collection	Accepted name*
1	Levada Ribeira da Janela	UMAD 0002	M.A.A.P. de Carvalho	1993	1
2	Levada Ribeira da Janela	UMAD 0003	M.A.A.P. de Carvalho	1994	1
3	Levada Ribeira da Janela	UMAD 0004	M.A.A.P. de Carvalho	1994	2
4	Levada Ribeira da Janela	UMAD 0005	M.A.A.P. de Carvalho	1994	1
5	Levada Ribeira da Janela	UMAD 0006	M.A.A.P. de Carvalho	1994	1
6	Levada Ribeira da Janela	UMAD 0007	M.A.A.P. de Carvalho	1994	2
7	Levada do Ribeiro Bonito	UMAD 0008	M.A.A.P. de Carvalho	1993	2
8	Lamaceiros, Santana	UMAD 0113	I. Vale Lucas	1994	2
9	Levada do Ribeiro Bonito	UMAD 0019	I. Vale Lucas	1994	1
10	São Jorge	UMAD 0101	I. Vale Lucas	1994	1
11	Levada do Ribeiro Bonito	UMAD 0021	I. Vale Lucas	1994	2
12	Santana	UMAD 0099	I. Vale Lucas	1994	2
13	Caniço	UMAD 0102	I. Vale Lucas	1994	2
14	Vale da Ribeira da Janela	–	I. Vale Lucas	1994	1
15	Vale da Ribeira da Janela	–	I. Vale Lucas	1994	1
16	Vale da Ribeira da Janela	UMAD 0103	I. Vale Lucas	1994	2
17	Vale da Ribeira da Janela	–	I. Vale Lucas	1994	2
18	Seixal, Porto Moniz	UMAD 0007	M.A.A.P. de Carvalho	1994	2
19	Ribeira Funda-Vereda	–	M.A.A.P. de Carvalho	1994	1
20	Ribeiro Funda-Vale Interior	–	I. Vale Lucas	1994	1
21	Vale da Ribeira da Janela	UMAD 0107	I. Vale Lucas	1994	2
22	Vale da Ribeira da Janela	UMAD 0008	I. Vale Lucas	1994	2
23	Vale da Ribeira da Janela	–	I. Vale Lucas	1994	2
24	Vale da Ribeira da Janela	–	I. Vale Lucas	1994	1
25	Vale da Ribeira da Janela	–	I. Vale Lucas	1994	1
26	Ribeiro Frio	UMAD 0009	I. Vale Lucas	1994	1
27	Vale da Ribeira do Marques	–	I. Vale Lucas	1994	2
28	Encosta da Ribeira do Marques	–	I. Vale Lucas	1994	2
29	Encosta da Ribeira do Marques	–	I. Vale Lucas	1994	1
30	Ilha, Santana	UMAD 0011	I. Vale Lucas	1994	2
31	Barreira, Santo António	UMAD 0012	I. Vale Lucas	1994	2
32	Ribeira da Achada do Marques	–	I. Vale Lucas	1994	1
33	Boaventura	–	R. Correia	1994	2
34	Boaventura	UMAD 0013	R. Correia	1994	2
35	Estrada da Boaventura	–	R. Correia	1994	2
36	Estrada da Boaventura	–	R. Correia	1994	2
37	Ilha		R. Correia	1994	1
38	Ilha	UMAD 0108	I. Vale Lucas	1994	1
39	Vale da Boaventura	UMAD 0104	I. Vale Lucas	1994	1
40	Silveira, Boaventura	UMAD 0105	I. Vale Lucas	1994	2
41	Levada do Castelejo-P. da Cruz	–	I. Vale Lucas	1994	1
42	Jardim Botânico	UMAD 0015	M. P. De Carvalho	1994	3
43	Jardim Botânico	UMAD 0016	M. P. De Carvalho	1994	2
44	Jardim Botânico	UMAD 0017	M. P. De Carvalho	1994	1
45	Ribeiro Frio	UMAD 0107	I. Vale Lucas	1994	1
46	Ribeiro Frio	–	I. Vale Lucas	1994	1
47	Levada do Ribeiro Bonito	UMAD 0018	I. Vale Lucas	1994	2
48	Levada do Ribeiro Bonito	UMAD 0019	I. Vale Lucas	1994	2
49	Levada Ribeira da Janela	UMAD 0020	I. Vale Lucas	1994	2

APPENDIX *Continued*

No.	Locality	Voucher number	Collector	Date of collection	Accepted name*
50	Vale da Ribeira da Janela	–	I. Vale Lucas	1994	2
51	Vale da Ribeira da Janela	UMAD 0021	M. P. de Carvalho	1995	1
52	Ribeira da Janela	UMAD 0022	M. P. de Carvalho	1995	2
53	Chão dos Louros, São Vicente	UMAD 0100	M. P. de Carvalho	1996	1
54	Jardim São Vicente	UMAD 0023	M. P. de Carvalho	1996	1
55	Jardim São Vicente	UMAD 0024	M. P. de Carvalho	1996	1
56	Encumeada	UMAD 0025	M. P. de Carvalho	1996	3
57	Levada do Ribeiro Bonito	UMAD 0026	R. Correia	1996	2
58	Santa, Porto Moniz	UMAD 0116	M. P. de Carvalho	1997	3
59	Santa, Porto Moniz	UMAD 0117	M. P. de Carvalho	1997	3
60	Santa, Porto Moniz	UMAD 0119	M. P. de Carvalho	1997	3
61	Santa, Porto Moniz	UMAD 0120	M. P. de Carvalho	1997	1
62	Santa, Porto Moniz	UMAD 0121	M. P. de Carvalho	1997	1
63	Santa, Porto Moniz	UMAD 0122	M. P. de Carvalho	1997	1
64	Santa, Porto Moniz	UMAD 0123	M. P. de Carvalho	1997	3
65	Lombo do Barbinhas	UMAD 0110	F. Fernandes	1998	3
66	Lombo do Barbinhas	UMAD 0111	F. Fernandes	1998	3
67	Lombo do Barbinhas	UMAD 0112	F. Fernandes	1998	3
68	Herbarium, Museu M. do Funchal	MADM	G. C. Costa	–	3
69	Herbarium, Museu M. do Funchal	MADM	G. C. Costa	–	3
70	Herbarium, Museu M. do Funchal	MADM	G. C. Costa	–	3
71	Herbarium, Museu M. do Funchal	MADM	G. C. Costa	–	3
72	Herbarium, Museu M. do Funchal	MADM	G. C. Costa	–	1
73	Herbarium, Museu M. do Funchal	MADM	G. C. Costa	–	3
74	Herbarium, Museu M. do Funchal	MADM	G. C. Costa	–	3
75	Herbarium, Museu M. do Funchal	MADM	G. C. Costa	–	3
76	Herbarium, Museu M. do Funchal	MADM	G. C. Costa	–	3
77	Herbarium, Museu M. do Funchal	MADM	G. C. Costa	–	1
78	Herbarium, Museu M. do Funchal	MADM	G. C. Costa	–	3
79	Jardim Botânico	–	M. P. de Carvalho	1999	3
80	Herbarium, Jardim Botânico	MADJ-05645	P. Nóbrega	–	3
81	Herbarium, Jardim Botânico	MADJ-02915	P. Nóbrega	–	3
82	Herbarium, Jardim Botânico	MADJ-05644	P. Nóbrega	–	3
83	Herbarium, Jardim Botânico	MADJ-06521	P. Nóbrega	–	3
84	Herbarium, Jardim Botânico	MADJ-05643	P. Nóbrega	–	3
85	Herbarium, Jardim Botânico	MADJ-05640	P. Nóbrega	–	1
86	Herbarium, Jardim Botânico	MADJ-05642	P. Nóbrega	–	1
87	Herbarium, Jardim Botânico	MADJ-07824	P. Nóbrega	–	3
88	Herbarium, Jardim Botânico	MADJ-07825	P. Nóbrega	–	3
89	Herbarium, Jardim Botânico	MADJ-07826	P. Nóbrega	–	2
90	Herbarium, Jardim Botânico	MADJ-05639	P. Nóbrega	–	1
91	Herbarium, Jardim Botânico	MADJ-05646	P. Nóbrega	–	1
92	Herbarium, Jardim Botânico	MADJ-10.10.95	P. Nóbrega	1995	3
93	Herbarium, Jardim Botânico	MADJ1-19.9.95	P. Nóbrega	1995	3
94	Herbarium, Jardim Botânico	MADJ-05631	P. Nóbrega	–	3
95	Fajã dos Vinháticos, S. de Água	UMAD 0200	R. Correia	1998	3
96	Levada da Ribeira da Janela	UMAD	M. P. de Carvalho	2000	3
97	Levada da Ribeira da Janela	UMAD	M. P. de Carvalho	2000	2
98	Levada da Ribeira da Janela	UMAD	M. P. de Carvalho	2000	3
99	Folhadal, Vale de S. Vicente	UMAD	M. P. de Carvalho	2000	3
100	Folhadal, Vale de S. Vicente	UMAD	P. Nóbrega	2000	3
101	Folhadal, Vale de S. Vicente	UMAD	F. Ganança	2001	3
102	Folhadal, Vale de S. Vicente	UMAD	F. Ganança	2001	2

APPENDIX *Continued*

No.	Locality	Voucher number	Collector	Date of collection	Accepted name*
103	Folhadal, Vale de S. Vicente	UMAD	N. Sousa	2001	3
104	Folhadal, Vale de S. Vicente	UMAD	N. Sousa	2001	3
105	Folhadal, Vale de S. Vicente	UMAD	F. Ganança	2001	3
106	Véu da Noiva, Seixal	UMAD	N. Sousa	2001	2
107	Véu da Noiva, Seixal	UMAD	N. Sousa	2001	2
108	Levada da Ribeira da Janela	UMAD	F. Ganança	2001	1
109	Fanal, Ribeira da Janela	UMAD	N. Sousa	2001	3
110	Levada da Ribeira da Janela	UMAD	N. Sousa	2001	3
111	Levada da Ribeira da Janela	UMAD	F. Ganança	2001	1
112	Levada da Ribeira da Janela	UMAD	F. Ganança	2001	2
113	Santa, Porto Moniz	UMAD	M. P. de Carvalho	2001	2
114	Levada da Ribeira da Janela	UMAD	F. Ganança	2001	1
115	Lombo do Barbinhas	UMAD	R. Correia	1999	3

*1, *Semele androgyna* (L.) Kunth ssp. *androgyna* P. de Carvalho; 2, *S. androgyna* (L.) Kunth ssp. *pterygophora* (Costa) P. de Carvalho; 3, *S. menezesi* (Costa) P. de Carvalho.